

RESEARCH ARTICLE

Root Inputs Influence Soil Water Holding Capacity and Differentially Influence the Growth of Native versus Exotic Annual Species in an Arid Ecosystem

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Abstract

Invasion by exotic annual species is increasingly impacting Southern California arid lands, altering ecosystem processes and plant community composition. With climate change, the Southwestern United States is expected to experience increasingly variable rainfall. Larger rainfall events could facilitate invasion by exotic species that can capitalize on high resource conditions. Exotic annual species also have dense shallow root systems that could create positive feedbacks to further invasion by increasing soil organic matter and water holding capacity. Alternatively, fine root inputs could create negative feedbacks to exotic plant growth if they stimulate microbial nutrient immobilization. The dual influences of rainfall regime and fine root inputs on species performance were evaluated in an experiment where native and exotic species were grown individually and in combination under varying watering regimes (large infrequent or small frequent pulses, holding total rainfall constant) and root

additions (with or without sterilized exotic roots). Mean soil moisture increased with larger infrequent watering events, and also with root addition. Plant growth (both native and exotic) increased with larger watering events, but declined with root addition. Exotic species growth declined more than native species growth with root additions. Mechanistically, root addition lowered inorganic nitrogen (N) availability, and microbial N immobilization increased with soil moisture content. Together these results show that increased fine root production promotes negative feedbacks to growth of exotic species via microbial N immobilization, especially under conditions of high soil moisture. Further, our results suggest that organic carbon additions are a potentially effective strategy for suppressing growth of problematic desert invaders.

Key words: carbon addition, climate change, invasion, nitrogen immobilization, water pulses.

Introduction

Exotic annual species are problematic invaders across western North America, especially in arid and semiarid regions (Mack 1981; Lovich & Bainbridge 1999; Craig et al. 2010), where they can negatively impact native species (Barrows et al. 2009) and alter ecosystem functioning by accelerating the fire regime (Brooks et al. 2004; Schiermeier 2005). Environmental changes such as altered climate and nitrogen (N) deposition may be facilitating these invasions, favoring exotic grasses over native desert species (Rao & Allen 2010). Invasions may become increasingly common in these areas because the Southwestern United States is expected to be a climate change “hot spot” in the coming decades, associated with increasingly variable rainfall patterns (Diffenbaugh et al. 2008). The abundance of exotic annual species often increases in high rainfall years (Bradley

& Mustard 2005; Hobbs et al. 2007), but we know much less about how native and exotic species respond to variation in the magnitude of rainfall events within years, although it has been predicted that more variable rainfall regimes will promote invasion (Knapp et al. 2008).

Positive plant–soil feedbacks may play an important role in facilitating the spread of problematic invaders (Levine et al. 2006). Exotic species can alter soil microbial communities (Klironomos 2002; Callaway et al. 2004), through inputs of allelopathic chemicals (Bais et al. 2003; but see Lind & Parker 2010), alteration of light availability via the litter layer (Lenz et al. 2003) or by altered nutrient cycling (Evans et al. 2001; Ehrenfeld 2003). One potential feedback mechanism that has been surprisingly untested is the role of root proliferation by exotic annual species, and subsequent additions of organic carbon (C) into soils. Exotic annual grasses often have high below-ground production of dense, fine roots (Holmes & Rice 1996), potentially creating a positive feedback, promoting invasion via by increasing soil water holding capacity. Alternatively, C additions in mesic systems often increase microbial activity and hence immobilization of limiting nutrients, suppressing the growth of exotic species and thus favoring native species (Blumenthal et al. 2003; Perry et al. 2010). The proliferation

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of fine root biomass associated with invasion by exotic annual species in arid and semiarid environments could thus lead to a mix of positive (via enhanced soil water holding capacity) and negative feedbacks (via microbial nutrient immobilization) to growth of exotic species.

Here we performed a greenhouse experiment to evaluate competition between exotic annual species and native desert forbs under varying soil moisture regimes, both with and without added fine root biomass. We tested the following hypotheses: (1) We expect all species have higher growth with higher soil moisture when grown individually, but exotic species will outperform native species when grown in competition under high soil moisture conditions. (2) Larger, less frequent precipitation events maintain high soil moisture and disproportionately benefit invasive species. (3) High root inputs from exotic species enhance soil water holding capacity, thus creating a positive feedback to enhance invasion success. (4) Alternatively, C inputs via the roots of exotic species could promote microbial activity, immobilize nutrients, and suppress plant growth. We evaluated these hypotheses for a suite of species commonly found in the arid lands of San Diego County, with the goal of evaluating two potential restoration strategies (C addition, seeding native species) to favor native species over problematic invaders.

Methods

The experiment was conducted in greenhouses at the University of California, San Diego Biological Field Station from January to April 2013. We selected four native focal annual wildflower species that commonly flower in San Diego County each spring, including *Amsinckia tessellata* (bristly fiddleneck), *Malacothrix glabrata* (desert dandelion), *Laesthenia californica* (California goldfields), and *Layia platyglossa* (tidy tips). We selected four problematic exotic species (designated by the California Invasive Plant Council) also common in San Diego County, including *Bromus hordeaceus* (soft brome), *Bromus madritensis* spp. *rubens* (red brome), *Erodium cicutarium* (redstem filaree), and *Schismus barbatus* (common Mediterranean grass). Each species was grown individually as well as together in the eight species mixture (competitive environment) in each watering regime (see treatment description below) and soil organic matter content (5 g sterilized exotic roots vs. no roots added) in a factorial block design ($n = 8$, for a total of 288 pots).

Pots were filled with commercially available native topsoil (sandy loam, Agri Service Inc., Vista, CA, U.S.A.). Exotic grass root biomass was collected from greenhouse-grown plants washed free of soil and sterilized by steam autoclaving. These roots were cut into approximately 1 cm pieces and 5 g of root biomass were mixed into the top 5 cm of soil in each pot in the root addition treatment. No roots were added to the control pots.

Seeds of the focal species were purchased commercially (S & S Seeds, Carpinteria, CA, U.S.A.) and germination percentages were evaluated on watered field soils prior to the start of the experiment. Each pot was sown with enough seeds to achieve a target of 24 individuals (three individuals of each species for

the pots where all eight species were grown in competition). Seeds were planted on 26 January and an initial pulse of 500 mL of water was added on 4 February. Seedlings of *E. cicutarium* (collected from the UC Elliot Chaparral Reserve) were transplanted on 7 February 2013 due to poor germination success in the greenhouse.

Subsequent watering was initiated on 9 February. The small, frequent watering regime added a 60 mL pulse of water every 5 days, and the large, infrequent watering regime added a 120 mL pulse of water every 10 days. Soil moisture measurements were taken daily during one 10-day watering cycle soon after seeds germinated using a Field Scout TDR 100 Soil Moisture Sensor (Spectrum Technologies, Aurora, IL, U.S.A.) measuring the volumetric water content. Pots were rotated in blocks every 2 weeks to account for spatial variation in greenhouse light availability. Watering continued for 47 days, at which time plants were harvested after showing signs of senescence. All aboveground biomass was harvested from each plot, dried for 48 hours at 40°C, and weighed.

The top 5 cm of soil were collected from each pot that contained all eight focal species, and sieved to remove roots and debris. Potassium chloride was used to extract soils for inorganic N (Keeney & Nelson 1982) and chloroform fumigation and extraction was performed to measure microbial biomass N (Brookes et al. 1985) and C (Beck et al. 1997). Potassium persulfate digestion (Delia et al. 1977) was used to oxidize all organic and inorganic N to nitrate, subsequently absorbance protocols (Doane & Horwath 2003) were used to determine the amount of nitrate in each sample.

Statistical Analysis

Statistical tests were performed with R version 2.15.0 (R Development Core Team 2013). Soil moisture was analyzed using a linear mixed-effect model (nlme R package, Pinheiro et al. 2014) with species origin (native, exotic, or mixed), watering regime (frequent or infrequent), roots (added or not added), and block as factorial fixed factors and individual pot ID as a random factor to account for repeated measures. The growth responses of the focal species were evaluated with a linear mixed-effect model where block, competitive environment (species grown individual vs. in combination), species origin (native or exotic), watering regime and roots were included as factorial fixed factors and species identity nested within origin was included as a random factor. Growth responses to the treatments were also assessed for each species individually using a linear model where competitive environment, water, and roots were included as factorial fixed factors and block as a random factor. Inorganic N, and microbial N and C were predicted with a linear model where the influence of watering regime and root treatments were factorially assessed with block position as a random factor. We performed type II analysis of deviance tests to assess statistical significance (car R package, Fox and Weisberg 2011). Tukey's Honest Significant Difference tests were performed as post hoc tests when interactions were identified.

When species were grown individually, pot biomass values were divided by eight, because one-eighth of the mass of seeds

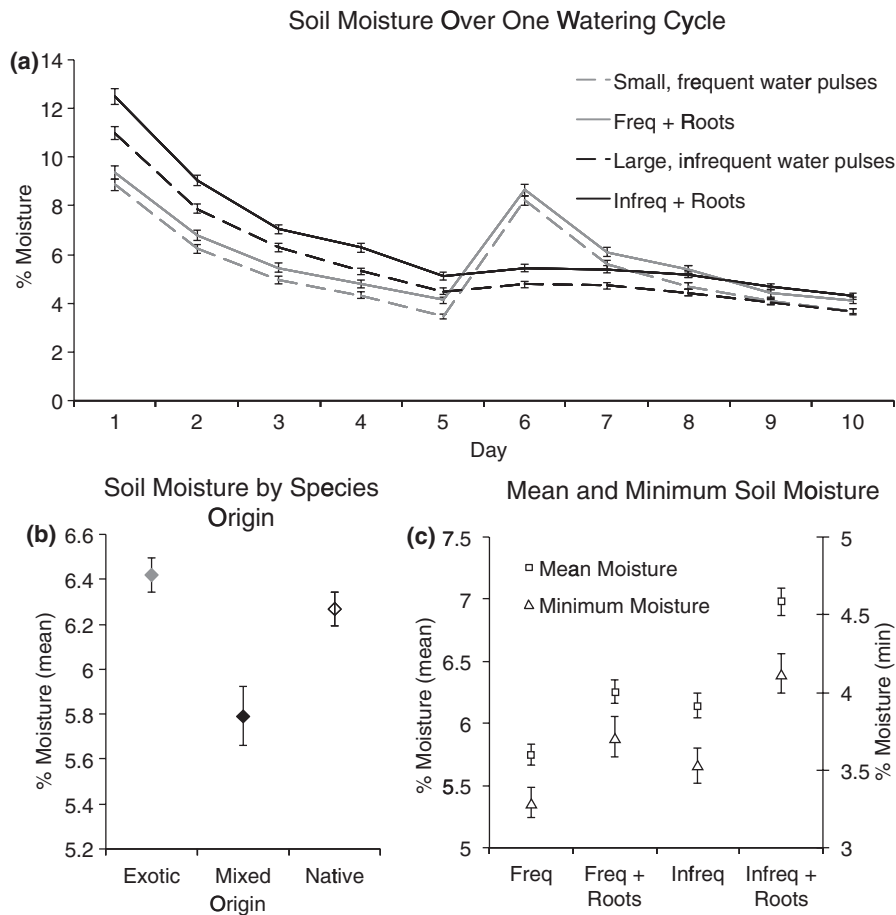


Figure 1. Mean and minimum soil moisture levels for one watering cycle (10 days), in each of the treatments manipulating watering regime and root additions. In the small frequent watering regime 60 mL of water was added every 5 days, whereas the infrequent watering regime received a single 120 mL pulse every 10 days.

of each focal species were sown in the eight species competition pots, as compared to the mass planted when each species was grown individually. Hence, in this analysis we compare the observed growth of species when grown in multispecies communities, and compare that value to the expected biomass of that species when grown individually and seeded at the same rate.

Additional information regarding the source and characterization of soils and roots used in this experiment are provided in the Supporting Information, along with all statistical tables.

Results

Pots supplemented with roots and watered with larger but less frequent events had higher mean (water $\chi^2_1 = 13.83, p < 0.001$; roots $\chi^2_1 = 19.82, p < 0.001$) and minimum (water $\chi^2_1 = 7.94, p < 0.001$; roots $\chi^2_1 = 19.53, p = 0.005$) soil moisture (Table S1, Supporting Information; Fig. 1b). Although we performed these measurements soon after germination at a time when we expected minimal impacts of plant growth on soil moisture, species composition had a small but significant effect on mean soil moisture, whereby the pots planted with all eight species

had slightly lower soil moisture (mixed moisture = 5.79%, exotic moisture = 6.42%, native moisture = 6.27%; origin $\chi^2_1 = 6.21, p = 0.045$; Fig. 1c).

Plant performance, as measured by biomass, was significantly influenced by watering regime, species origin, and root additions, with interactions (Table S1; Fig. 2). Watering with large, infrequent events increased plant biomass (watering regime $\chi^2_1 = 25.60, p < 0.001$) and this effect was greater for exotic species (origin \times water $\chi^2_1 = 4.76, p = 0.029$). In contrast, root addition decreased overall plant biomass (root addition $\chi^2_1 = 3.89, p = 0.049$). When roots were added there was little difference between exotic and native plants, although exotics produced significantly higher biomass when grown without root additions (root \times origin $\chi^2_1 = 4.41, p = 0.036$). Block was a significant effect in our analysis ($\chi^2_7 = 53.24, p < 0.001$), because one block had consistently lower biomass due to unknown factors (data not shown).

Most species had higher biomass (standardized by seeding rate) when grown alone than when grown in combination (significant only for the native *Malacothrix glabrata*, and exotics *Erodium cicutarium*, and *Bromus hordeaceus*; Table S2, Fig. 3). However, both the native forb *Amsinckia tessellata* and the

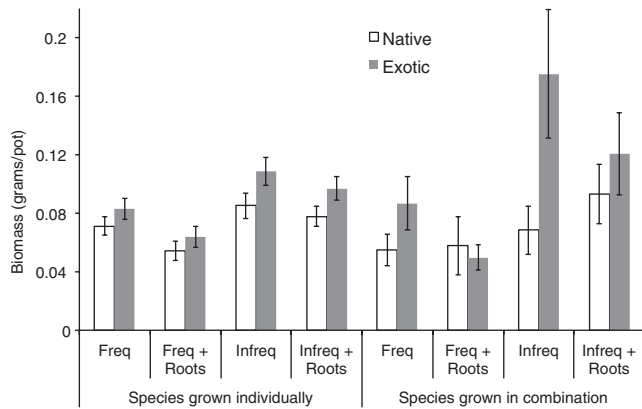


Figure 2. Aboveground biomass (mean + SE) for native and exotic species grown individually and in competition, for each treatment combination of root addition and watering frequency. Note biomass values are averaged across species to illustrate the statistical significance of the factors in the analysis.

exotic grass *Schismus barbatus* showed higher biomass when grown in combination with other species (competitive environment: *A. tessellata* $\chi^2_1 = 5.04$, $p = 0.25$; *S. barbatus* $\chi^2_1 = 27.17$, $p < 0.001$; Fig. 3a & 3e). Species also displayed variation in their responses to the experimental treatments. Qualitatively, *S. barbatus* and *A. tessellata* showed the most growth under all treatments compared with other species when grown in competition, suggesting that their responses likely drove the exotic and native species responses respectively (Table S2; Fig. 3). Growth of *S. barbatus* was promoted by infrequent watering, and this effect was greater in the pots where all species were grown in combination (water \times competition $\chi^2_1 = 6.08$, $p = 0.014$; Table S2, Fig. 3e). *Schismus barbatus* declined with root addition in the combination pots but not when grown alone (root \times competition $\chi^2_1 = 6.47$, $p = 0.011$). Infrequent, large watering events also increased growth for *B. madritensis*, *B. hordeaceus*, *Laesthenia californica*, *M. glabrata*, and *E. cicutarium*, although this effect was only significant for the latter two species when grown individually (Table S2; Fig. 3). *Erodium cicutarium* showed higher growth when roots were added in combination pots; however, when grown individually the species had higher growth when no roots were added (root \times competition $\chi^2_1 = 4.20$, $p = 0.040$).

Inorganic N availability in soils at the end of the experiment was significantly influenced by an interaction between root addition and watering regime (root \times water $\chi^2_1 = 5.15$, $p = 0.23$; Table S3); root addition decreased soil inorganic N availability, and this effect was strongest in pots with large but infrequent watering events. Microbial biomass N concentrations were also higher in pots with infrequent watering treatments (water $\chi^2_1 = 13.97$, $p < 0.001$; Table S3, Fig. 4). Treatments had no significant effects on microbial biomass C (water $\chi^2_1 = 0.45$, $p = 0.505$; Root $\chi^2_1 = 0.05$, $p = 0.825$; root \times water $\chi^2_1 = 1.04$, $p = 0.308$; Table S3).

Discussion

We found that larger, infrequent watering events maintained higher average soil moisture than when the same water quantity was applied in small, frequent events, potentially because larger watering events allowed water to reach deeper soil layers, hence minimizing evaporative loss (Fay et al. 2008). Higher soil moisture in turn increased plant biomass; these results are consistent with a prior study in a semiarid grassland that found larger infrequent rainfall events tended to increase soil moisture and plant growth (Heisler-White et al. 2009). The large, infrequent watering treatment in our experiment disproportionately increased the growth of exotic species, supporting our hypothesis that exotic species would outperform native species under higher soil moisture. Although exotic annual species can have dramatically positive responses to years of high rainfall (e.g. Hobbs et al. 2007), some studies have found no impact of soil moisture on direct competition between native and exotic species (Maron & Marler 2008), suggesting that exotic species may not always benefit more than native species from high soil moisture.

We also found that root addition increased mean soil moisture content, consistent with prior studies showing that increasing soil organic matter content can increase soil water holding capacity (Blumenthal et al. 2003); however, the increase in soil moisture caused by root addition did not increase plant growth. Instead, root addition suppressed plant growth. Our analysis showed root addition suppressed exotic species as a group more than native species (although this was likely driven by the significant response of one species—*Schismus barbatus*). Microbial biomass N increased with infrequent watering, suggesting that larger water pulses stimulated microbial activity to a greater degree (e.g. Austin et al. 2004). Inorganic N was reduced under infrequent watering and root addition, consistent with the idea that soil microbes immobilize inorganic N when C was added in the form of fine roots. Adding C to soils in mesic systems often causes soil microbes to immobilize N, favoring the growth of native species (Alpert & Maron 2000; Blumenthal et al. 2003). Thus, root addition in our study may have favored slower growing native species over fast growing exotic species by limiting the available N in the soil (Bobink 1991; Alpert & Maron 2000; Perry et al. 2010). Our results show that this effect was greatest when soil moisture was high (infrequent but larger watering events). In a study similar to ours, Blumenthal (2009) found that C additions in concert with water addition reduced invasive plant growth in a semiarid grassland system. Further, the results of this study are consistent with C addition studies in the Mojave Desert, showing that C amendments can stimulate increased microbial N immobilization even under xeric conditions (Steers et al. 2011).

As a group, we found that exotic species in our experiment tended to suppress the growth of native species competitively, but there was significant variation among our focal species in their responses. In particular, *Amsinckia tessellata* had the highest growth among the native species when grown in competition (Fig. 3a), and actually had higher biomass when grown in combination than when grown alone, suggesting this species was

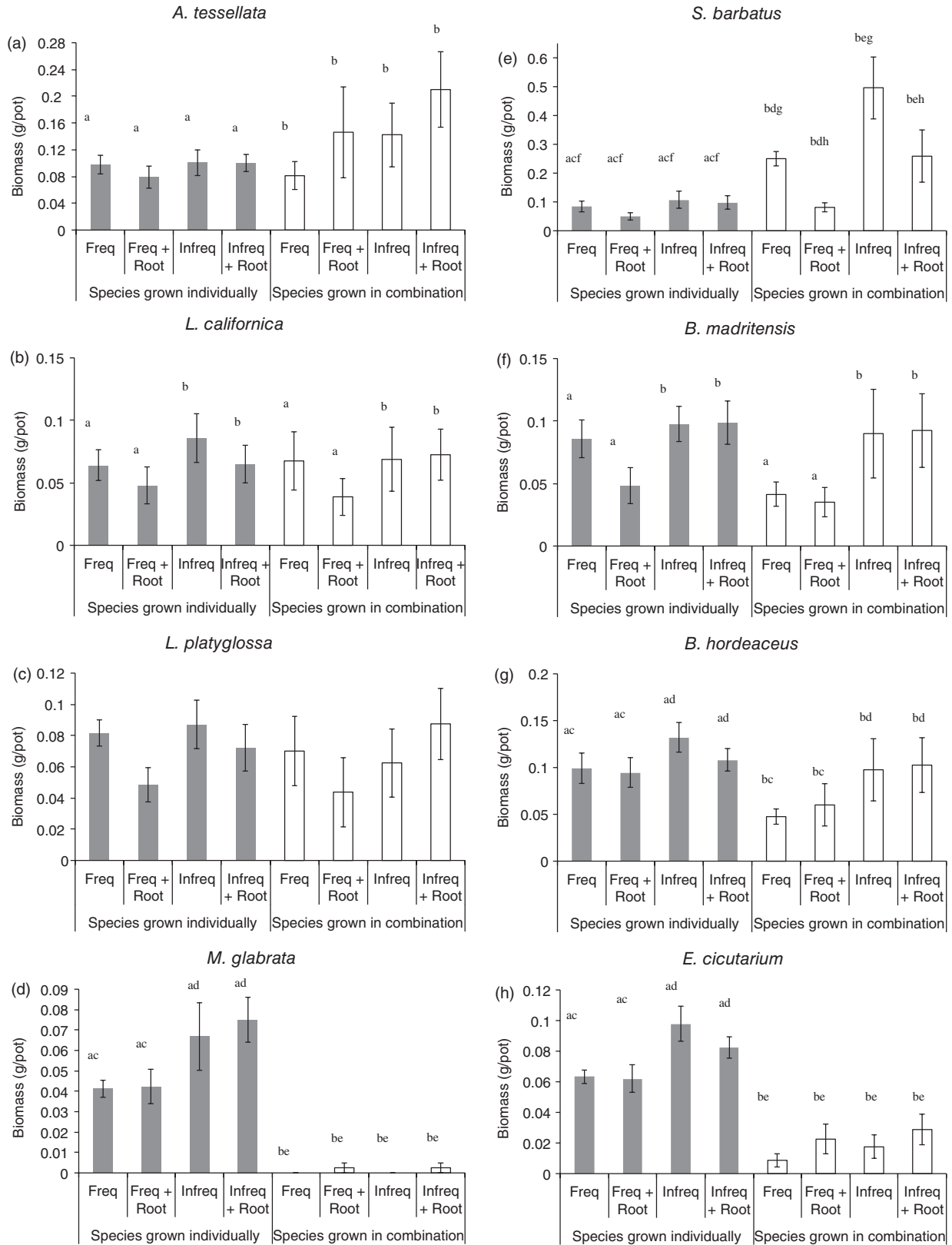


Figure 3. Aboveground biomass responses to varying watering regime and root addition treatments for native (a–d) and exotic (e–h) species grown individually (gray) or in interspecific competition with the other focal species (open).

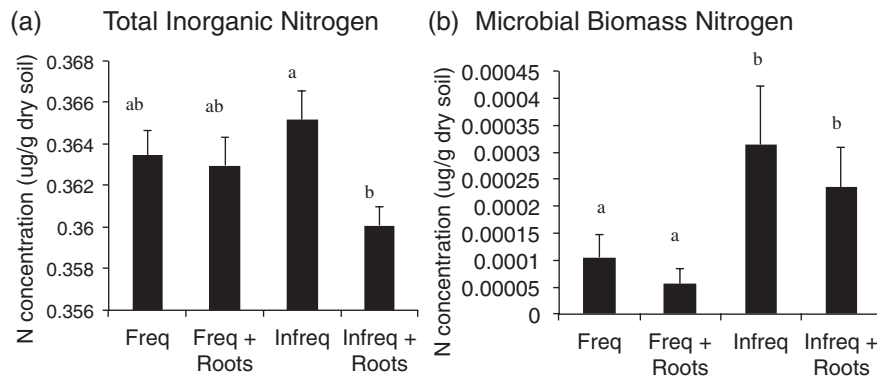


Figure 4. Concentrations of soil extractable inorganic nitrogen (a) and microbial biomass nitrogen (b) for combination of watering regime and root addition treatments. Letters distinguish significant differences between means based on post hoc tests.

facilitated by growing in a diverse community. Other studies have also found that *A. tessellata* was robust to exotic competition (Brooks 2009; Abella et al. 2011), potentially due to traits such as large seed size and early-season germination (Salo et al. 2005). Hence, *A. tessellata* could be an effective choice for restoration efforts attempting to establish native cover via seeding, especially when there may be potential competition from exotic species present in the seedbank.

There was also variation among the exotic focal species in their responses to the experimental treatments, with potential implications for management of these problematic invasive species. *Erodium cicutarium* growth was significantly suppressed when grown in the multispecies competitive environment, suggesting that seeding native species can be an effective strategy for reducing the abundance of this common desert invader. Growth of *E. cicutarium* was also reduced by low soil moisture (small, frequent watering treatment). This species is a common invader of many arid systems but has been shown to decline substantially in drought years (Blackshaw et al. 2000). Our results suggest that restoration efforts employing irrigation to promote germination of native seeds should be cautious to prevent overwatering in areas where *E. cicutarium* could be present in the seedbank, as high soil moisture favors this exotic species over the common native species used in this experiment. Timed herbicide applications have also been found to be effective for managing this particularly early-active species, and are more effective for increasing native cover than management efforts such as weeding that disturb soils (Marushia et al. 2010).

Schismus barbatus is a common exotic grass in Southern California deserts (Brooks 1999) and was the dominant species in pots where our eight focal species were grown in competition. Further, biomass (scaled for seeding rate) was higher for this species when grown with multiple species than when grown in a monoculture; hence, efforts to reseed native species are unlikely to be successful if this strong competitor is present in the seedbank. However, *S. barbatus* growth was significantly lowered by root addition, suggesting that organic C addition could be a feasible management strategy to combat invasions of *S. barbatus*. This problematic invader has been shown to benefit from N enrichment (DeFalco et al. 2001; Brooks 2003), and a

study that used sucrose additions similarly found that labile C additions reduced growth of *S. barbatus* under field conditions (Steers et al. 2011), thus C additions are a logical management strategy with the potential to lower N availability and hence the competitive dominance of this species.

Management efforts focused on reducing soil N availability have generally used sawdust or mulch as sources for C addition (Wilson & Gerry 1995; Zink & Allen 1998; Alpert & Maron 2000; Paschke et al. 2000; Blumenthal et al. 2003). The results of this study suggest that the biomass of exotic annual species could be left in situ as a C source, provided it is harvested before the plants set seed, and there is not a danger of resprouting from intact root stocks. However, exotic litter can be a fuel source promoting fire, and so fuel reduction is a major goal for many land managers (Brooks et al. 2004); hence management efforts aimed at maintaining litter with the goal of lowering soil N availability would need to consider associated fire risks of this strategy. Additionally, the timing of C amendments could be important: Early-season C amendments are likely to suppress exotic annual species disproportionately in this region (Salo 2004), because they generally have flexible germination cues that allow them to emerge earlier and faster at the start of the growing season (Wainwright & Cleland 2013). Consistent with this idea, Steers et al. (2011) found that C amendment reduced exotic annual grass abundance most in a year when they germinated first, whereas native species and exotic annual forbs were impacted in a year when the timing of C amendment coincided with their emergence.

Overall, the results of this study demonstrate how inputs of organic C from the fine roots of exotic species can initiate a complex set of positive and negative feedbacks to invasion, and that the outcome of these interactions depends on environmental context (rainfall regime), biotic interactions (interspecific competition), and species identity. In particular, although we found that exotic species benefited more from high soil moisture (resulting from larger, but less frequent watering events), exotic species growth declined more than native species when roots were added to soil, even though root additions also increased soil moisture. This shows that in this case, the negative effect of microbial nutrient immobilization outweighed the positive

influence of increased soil moisture for plant growth when exotic roots were added to soil. Although our results highlight general mechanistic feedbacks that may be applicable for understanding the outcome of invasions in many systems, we also found significant variation among species in their responses to our experimental treatments—both within and between groups based on native versus exotic origin—that may aid in identifying effective management strategies for particularly problematic desert invaders.

Implication for Practice

- Carbon additions in arid environments can reduce exotic plant growth via enhanced microbial nutrient immobilization; this effect varies among species and is greatest when soil moisture is high.
- *Schismus barbatus* growth was significantly suppressed by C addition, suggesting this would be a successful strategy to suppress growth of this invasive species.
- *Erodium cicutarium* was suppressed by interspecific competition, suggesting that seed addition could be a strategy to combat this problematic invader.
- *Amsinckia tessellata* was a strong competitor with exotic plant species; this widespread species is found in a variety of arid and semiarid California vegetation types, suggesting this species is a prime candidate for seeding in restoration.

Acknowledgments

We thank E. Allen for constructive comments on an earlier version of this manuscript. We are grateful for help in analysis of soil samples provided by E. Esch and P. Magali. J. G. M. was partially supported by NSF DEB #1154082.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Supplementary methods and statistical tables

Table S1. ANOVA results showing the response of biomass, mean pot soil moisture, and minimum pot soil moisture to the experimental treatments.

Table S2. ANOVA results for exotic and native species biomass for given treatments and their interactions.

Table S3. ANOVA results for soil analysis on inorganic nitrogen, microbial biomass nitrogen, and microbial biomass carbon.